Article:

Cowley, M J R, Thomas, C D orcid.org/0000-0003-2822-1334, Thomas, J A et al. (1 more author) (1999) Flight areas of British butterflies: assessing species status and decline. Proceedings of the Royal Society B: Biological Sciences. pp. 1587-1592. ISSN 1471-2954

https://doi.org/10.1098/rspb.1999.0819

THE ROYAL SOCIETY

Flight areas of British butterflies: assessing species status and decline

M. J. R. Cowley[1*], C. D. Thomas[1], J. A. Thomas[2] and M. S. Warren[3]

[1]*Centre for Biodiversity and Conservation, School of Biology, University of Leeds, Leeds LS2 9JT, UK*
[2]*Institute of Terrestrial Ecology, Furzebrook Research Station, Nr Wareham, Dorset BH20 5AS, UK*
[3]*Butterfly Conservation, PO Box 444, Wareham, Dorset BH20 5YA, UK*

Geographical range size is a key ecological variable, but the consequences of measuring range size in different ways are poorly understood. We use high-resolution population data from British butterflies to demonstrate that conventional distribution maps, widely used by conservation biologists, grossly overestimate the areas occupied by species and grossly underestimate decline. The approximate flight areas occupied by 20 out of 45 colonial British species were estimated to cover a median of only 1.44% of the land surface within occupied regions. Common species were found to be declining faster than conventional distribution maps suggest: common and rare species had no significant difference in their population-level rates of extinction. This, combined with the log-normal form of the range-size frequency distribution, implies that species-level extinction rates may accelerate in the medium to long term. Population-level conservation is a matter of great urgency for all species, not just for the rarest.

Keywords: conservation; extinction; range size; IUCN

1. INTRODUCTION

Geographical range size is a key ecological variable. It is used widely by conservation biologists to draw up species red lists, measure rates of decline, identify areas of endemism and locate 'hot spots' of diversity (Vane-Wright *et al*. 1991; Groombridge 1992; Prendergast *et al*. 1993; Gaston 1994, 1996, 1998; Thomas & Abery 1995; Quinn *et al*. 1997; Warren *et al*. 1997; Kunin 1998). For practical reasons, species ranges are commonly plotted as presence–absence in $10\,\mathrm{km} \times 10\,\mathrm{km}$ grid squares in northern Europe, in 50 km or coarser grids in less heavily researched parts of the world and as relatively crude range maps in field guides. It is widely accepted that species may populate only a small proportion of 'occupied' areas, but the need for rapid conservation policies and actions has already driven widespread use of these data (Vane-Wright *et al*. 1991; Groombridge 1992; Prendergast *et al*. 1993; Gaston 1994; Quinn *et al*. 1997; Warren *et al*. 1997; Kunin 1998). Therefore, the consequences of measuring range areas in different ways should be quantified (Gaston 1994; Thomas & Abery 1995; Warren *et al*. 1997; Kunin 1998). How large an area does a species actually populate within each 'occupied' grid square and what are the implications for conservation?

Grid square distribution maps have provided evidence of butterfly decline in Britain (Heath *et al*. 1984) and coarse grain maps do identify declines in rare species (Thomas & Abery 1995). However, common species, which may have many populations per occupied square, have the potential to decline considerably within squares before they are lost from entire squares (Thomas & Abery 1995). Thus, it has been suggested that common species in Britain have declined just as much as some of the rarities (Heath *et al*. 1984), but this has never been quantified.

For most insects, the size of the area populated (Mace & Lande 1991; IUCN 1994), rather than population size, is an appropriate way of assessing current status and potential threats because high-density populations can become extinct rapidly through natural population variability, successional dynamics or habitat loss and modification (Samways 1994; Lawton & May 1995; Hughes *et al*. 1997). Habitat area is also known to be a good predictor of extinction probability in butterfly populations (Thomas 1994; Thomas & Hanski 1997).

In this paper, we analyse flight (or habitat) areas populated by colonial British butterflies. We examine the differences between (i) areas deemed to be occupied by species when measured as flight area compared with grid square occupancy, and (ii) decline measured using a flight area approach and decline measured using a conventional grid square approach.

2. METHODS

(a) *Flight areas*

Flight areas represent land units within which adults mate, obtain adult resources and lay eggs. The entire immature life cycle is also completed within their bounds. Thus, flight areas represent natural population units that could be secured and managed for conservation. We use the term 'flight area' rather than 'habitat area' so as not to presume which factors are most important in determining the local distributions of each species and because some suitable habitats may not be populated.

*Author for correspondence (bgymjrc@leeds.ac.uk).

Received 22 April 1999 *Accepted* 19 May 1999

Nonetheless, the boundaries of most flight areas do correspond to identifiable changes in habitat.

We only consider species that have been classified as having 'closed' populations (Thomas 1992; Warren 1992) and exclude highly mobile species that fly widely through the landscape. For these mobile species, it is not possible to identify distinct areas of occupied habitat. The word closed gives the misleading impression that butterflies never leave their natal habitats, so we have chosen instead to use the term 'colonial'. Individuals of colonial species may sometimes wander away from breeding habitats or move between breeding areas, but most individuals spend most of their time within these habitats and many of them exist as metapopulations (Thomas & Hanski 1997). For some of the species, a high proportion of individuals may move between habitat patches, but most individuals will nonetheless spend most of their adult lifetime (and all of their immature life stages) within distinct areas of habitat. Thus, identification of colony limits is practicable (J. A. Thomas 1983). Area estimates may be affected slightly by variation in mobility and density, as more mobile and higher density species might appear to occupy larger areas. However, these errors will probably be small (relative to the range of area estimates across all species).

(b) *National flight areas for conservation priority species*

Thirteen out of 23 conservation priority (Warren *et al*. 1997) butterfly species in Britain have been subject to partial (regional) or complete (national) population-level mapping (table 1). For these species, every known population within the sample area has been visited, the approximate colony boundaries mapped and the extent of their flight areas calculated. For *Euphydryas aurina* and *Satyrium pruni*, 39 out of 374 and 22 out of 44 known populations were sampled, respectively.

(c) *Regional flight areas*

To produce regional flight area estimates for a range of other species, we (i) intensively sampled 35 km^2 of lowland north Wales (the Creuddyn Peninsula around Llandudno), calculating the total area covered by all major habitat types, and (ii) in 1997 conducted over 2000 butterfly transect counts, stratified by habitat type, to establish species–habitat associations. Combining (i) and (ii) allowed us to estimate areas of occupancy for each species in the study region (table 2). Distributions in the same area were mapped at 500 m resolution, based on national Ordnance Survey (1994) maps, using over 14 000 distributional records between 1996 and 1998 in addition to records derived from the transects. Again, all of the species included in this analysis are regarded as colonial, so it was quite practicable to identify 'occupied' habitat units.

The area was divided into major vegetation types (table 3) according to phase 1 land-cover classes (Joint Nature Conservation Committee 1990), supplemented with other habitat types that are of particular relevance to butterflies, such as woodland edge and woodland ride. All vegetation types were drawn onto a 1:10 000 Ordnance Survey (1994) map and the area of each was calculated using the Trabecular Analysis System (TAS 1.2) image analysis system (© Steve Paxton 1994, 1995). To determine the species–vegetation associations, one 300 m long butterfly transect was located in each of approximately ten samples of every vegetation type, spread across the entire landscape (within the constraints of the distribution of each vegetation type). Transects were monitored every other week from April to October 1997 using standard methods (Pollard & Yates 1993). Species were defined as present on a transect if more than two individuals were counted during the sampling period. Singletons were excluded to prevent occasional vagrant individuals affecting our assessments of patterns of vegetation association. The proportions of 'occupied' samples were assumed to reflect the occupancy of each vegetation type at a regional scale.

Although many butterflies have much more specific habitat requirements than simply the presence of a particular (coarse) vegetation category, our stratified sampling approach should not be biased with respect to area estimation. For example, if a species occupied only half of the samples of a particular vegetation type because the butterfly required a particular host plant to be present or for the vegetation to occur on south-facing slopes, then only half of the total area of that vegetation category would be included in the area estimate for that species. Furthermore, the distribution of these same habitat types can be used to predict successfully the distributions and densities of individual butterfly species within the study region (Cowley *et al*. 2000).

The Creuddyn Peninsula study region is at low elevation and is coastal. It is a pastoral landscape and contains a variety of rural and urban habitats, but lacks arable fields and includes high-diversity limestone grassland and sand dunes. Most butterfly species can therefore be expected to cover a higher percentage of this landscape than the average for lowland Britain.

(d) *Estimates of regional population-level decline*

Using an approach based on flight areas, we estimated decline for each species in our Welsh landscape. To do this, we assumed current butterfly–vegetation associations, combined with definite and estimated land-use change since 1901. The extents of nine vegetation categories, including urban, woodland and coastal dune, were calculated directly from Ordnance Survey (1901) maps. The extent of 1901 limestone grassland was calculated according to the present extent of limestone grassland, plus the size of woodland and urban area that has since developed on limestone outcrops.

The remaining habitats were increased in proportion to their relative extents in the current landscape to occupy the area that has since become urbanized. The final step was to assume all the present 'improved' grassland was 'semi-improved' grassland in 1901. This is consistent with documented habitat change in other parts of the country (Fuller 1987).

3. RESULTS AND DISCUSSION

(a) *Assessment of species status*

The national flight areas for butterfly species sampled throughout Britain were consistently small, with a median of 9 km^2 estimated to be occupied: four out of the eight species occupied <3 km^2 or $<0.001\%$ of the entire British land surface (table 1). The remaining five species in table 1 were also highly localized, but surveys were carried out only in specific regions within their British distributions. If the results for these five species can be extrapolated from occupied 10 km grid squares in the sample regions to all 10 km grid squares occupied by these species in Britain (this has unknown error because these species may have been surveyed in areas where they were unusually common or rare), the median area occupied by them would be 27 km^2. The species in table 1

Table 1. *Flight area estimates and 10 km grid square area for high and medium conservation priority species in England, Wales and Scotland*

(*Satyrium pruni* is known to occupy 44 woodlands; 21 of these woodlands were sampled and the total extent of all colonies was found to be 0.9 km^2. The mean area occupied per woodland was 0.04 km^2. *Euphydryas aurina* is known to occur at 374 sites; 39 sites were sampled and the mean area of these colonies on these sites was 0.06 km^2.)

species name	number of 10 km grid squares occupied	percentage of 10 km grid squares sampled	percentage of the land surface occupied in sample area	total area occupied by flight areas in Britain (km^2)	percentage of the British land surface occupied	location of studies
high-priority species						
Carterocephalus palaemon	31	100	2.00	62.0	0.0300	all known colonies (Ravenscroft 1993)
Hesperia comma	24	100	0.10	2.1	0.0009	all known colonies (Thomas *et al.* 1986)
Aricia artaxerxes	71	7	0.04	—	—	north-east England (S. Ellis, unpublished report)
Argynnis adippe	105	100	0.10	15.0	0.0070	all known colonies (Warren *et al.* 1995)
Euphydryas aurinia	207	10% of colonies	—	22.0	0.0100	sample of all known colonies (Warren 1994)
Mellicta athalia	13	100	0.20	2.6	0.0010	all known colonies (M. S. Warren, unpublished report)
medium-priority species						
Thymelicus acteon	13	100	1.20	15.0	0.0070	all known colonies (G. Pearman, B. Goodger, N. A. D. Bourn and M. S. Warren, unpublished report; J. S. Thomas, R. W. Smith, D. J. Simcox and C. D. Thomas, unpublished report)
Satyrium pruni	24	48% of colonies	—	1.9	0.0008	sample of all known colonies (J. A. Thomas, unpublished report)
Cupido minimus	197	6	0.10	—	—	Dorset (J. A. Thomas, R. W. Smith, D. J. Simcox and C. D. Thomas, unpublished report)
Plebejus argus	104	7	0.50	—	—	north-west Britain (C. D. Thomas 1983)
Lysandra bellargus	79	9	0.30	—	—	south-east Dorset (G. Pearman, B. Goodger, N. A. D. Bourn and M. S. Warren, unpublished report; J. A. Thomas, R. W. Smith, D. J. Simcox and C. D. Thomas, unpublished report)
Melitaea cinxia	6	100	0.10	0.6	0.0003	all known colonies (D. J. Simcox and J. A. Thomas, unpublished report)
Coenonympha tullia	293	4	1.80	—	—	Cumbria and Northumbria (Eales 1996; Wain 1997)

include the majority of the most localized species in Britain, but they nonetheless comprise 13 out of all 45 (29%) colonial butterfly species in Britain.

According to IUCN (1994) criteria for identifying threat, based on area of occupancy (Mace & Lande 1991) and applied to Britain as a region, the 13 species qualify as critically endangered (five spp. occupy <10 km^2), endangered (seven spp. occupy 10–500 km^2) or vulnerable (one spp. occupies 500–2000 km^2). In addition to a simple measurement of area, the IUCN (1994) criteria also require species to meet two out of the following three criteria: severe fragmentation, continuing decline and extreme fluctuations (Mace & Lande 1991). These species generally fulfil the first and third of the criteria and most of them also fulfil the second (Warren *et al.* 1997). Using 10 km^2 occupancy, only zero, zero and three of these species would fall into these three categories, respectively: coarse-grained data grossly overestimate current status (Thomas & Abery 1995).

At a regional level and in a generally high-quality landscape for butterflies, seven out of 15 (47%) species occupied less than 1 km^2 (<3%) of the landscape

Table 2. *The percentage occupancy of species in the North Wales study region*

species name	percentage of British 10 km grid squares occupied	percentage of regional 500 m grid squares occupied	percentage of present regional landscape occupied by flight areas	percentage of estimated previous regional landscape occupied by flight areas	change in area of occupancy (%)
regionally extant species					
Aphantopus hyperantus [a]	48	6	0.007	—	—
Thymelicus sylvestris [a]	50	22	0.07	—	—
Argynnis aglaja	30	26	0.3	0.5	−41.0
Lycaena phlaeas	76	66	1.0	15.0	−90.6
Erynnis tages	24	7	1.44	1.58	−8.7
Ochlodes venata	56	46	2.0	9.0	−74.8
Lasiommata megera	64	41	2.0	2.6	−11.6
P. argus	5	16	3.0	3.4	−16.9
Hipparchia semele	27	41	5.0	13.0	−60.0
Aricia agestis	16	53	10.0	44.0	−76.6
Coenonympha pamphilus	82	48	11.0	22.0	−49.4
Polyommatus icarus	86	92	13.0	51.0	−74.9
Pararge aegeria	44	72	14.0	46.0	−70.2
Pyronia tithonus	51	96	16.0	59.0	−73.3
Maniola jurtina	96	99	41.0	89.0	−53.9
regionally extinct species					
Callophrys rubi	27	0	0.0	?	−100.0
C. minimus	9	0	0.0	?	−100.0
Hamearis lucina	18	0	0.0	?	−100.0
Boloria selene	30	0	0.0	?	−100.0
Boloria euphrosyne	14	0	0.0	?	−100.0
A. adippe	5	0	0.0	?	−100.0
Argynnis paphia	18	0	0.0	?	−100.0

[a] Species with expanding range margins for which the historical reconstruction would not be appropriate.

(table 2). This increases to 14 out of 22 (64%) species if one includes regionally extinct species (Williams 1864; Ellis 1950). Thirty-two per cent of the species recorded from this region have already become extinct and approximately one-half of the surviving species could potentially be endangered.

(b) *The disparity between flight area occupancy and grid square occupancy*

If the results from tables 1 and 2 are taken together (table 1 species nationally extant in 10 km^2 and in table 2 regionally extant species in 35 km^2), the flight areas covered a median of only 1.44% of the land surface within 'occupied' areas. Moreover, for the same species studied in the same areas, the mean flight areas per 'occupied' area were correlated with national 10 km^2 range sizes (from Heath *et al.* 1984), showing that geographically restricted species (at a coarse scale) are particularly localized within their distributions (figure 1). A comparable pattern was observed at the regional scale in North Wales. In this case, the exaggeration in area deemed to be occupied, based on a 1 km grid, was greatest for species with relatively small flight areas (exaggeration is calculated by the grid area estimate divided by flight area; Spearman's rank correlation for exaggeration versus flight area $= -0.97$, $n = 15$, and $p = < 0.0001$).

The coarser the grid that is placed over the landscape, the greater the exaggeration of species range sizes: this problem is particularly acute for rare species (Kunin 1998). When placing 500 m, 1 km and 2 km grids across the landscape of North Wales, the degree of exaggeration was found to increase with grid size. The slope of this increase (plots of log exaggeration versus log grid area for each species) was negatively correlated with flight area (figure 2): thus, increasing grid size disproportionately

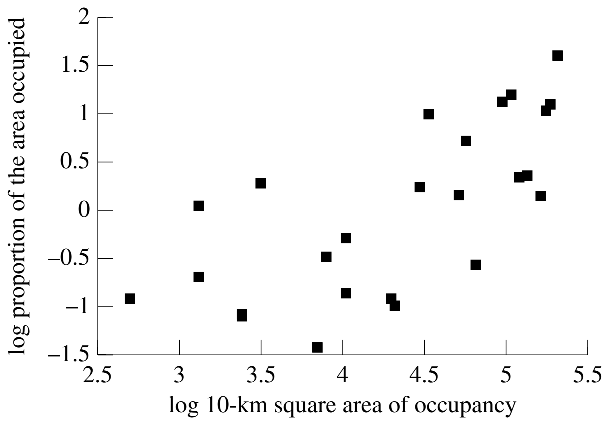

Figure 1. The relationship between British 10 km distribution size ($\log_{10}$ 10 km^2 area of occupancy) and the proportion of the land surface that is covered by flight areas within the distribution ($\log_{10}$ mean proportion of area 'occupied') ($y = -3.32 + 0.77x$, $r^2 = 0.48$ $n = 25$ and $p < 0.001$). Nationally localized species (x-axis) are particularly localized within their ranges (y-axis).

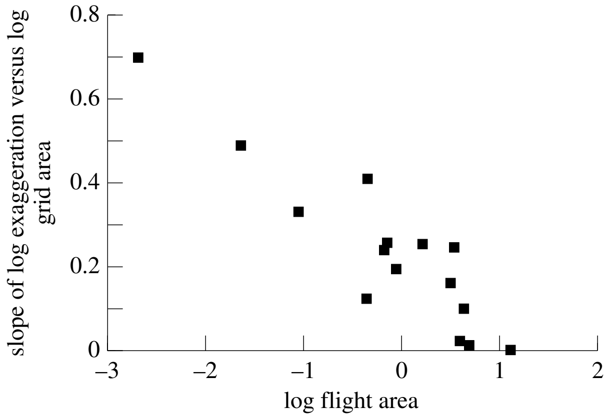

Figure 2. The effect of grid size on the degree to which grid-based maps exaggerate distribution sizes (slope of $\log_{10}$ exaggeration versus $\log_{10}$ flight area, where exaggeration is calculated by the grid area estimate divided by flight area) plotted against the flight areas of each species (Spearman's correlation $= -0.84$, $n = 15$ and $p < 0.0001$). Coarse grids differentially exaggerate range area estimates for rare species.

Table 3. *The total area (ha) of the landscape occupied by major habitat types in the North Wales study area in 1997 and estimated for 1901*

habitat types	area 1997	%	area 1901	%
amenity grassland	53	1.50	0	0.00
bracken	43	1.22	72	2.09
coastal dune	15	0.42	88	2.54
ditches	6	0.17	10	0.30
heathland	44	1.26	72	2.09
hedgerows	69	1.98	103	2.95
improved grassland	1100	31.43	0	0.00
lane	14	0.40	21	0.60
limestone grassland	221	6.31	242	6.96
non-habitat[a]	541	15.47	519	14.92
semi-improved grassland	78	2.26	2015	57.98
scrub	84	2.41	88	2.53
urban areas	987	28.21	40	1.16
verges	987	0.47	0	0.00
woodland	206	5.87	185	5.33
woodland edges	21	0.60	19	0.55
woodland rides	0	0.01	0	0.01

[a]Includes salt marsh, scree and some cliff–quarry faces.

exaggerated area estimates for species with relatively small flight areas.

(c) *The assessment of population-level decline*

We already know that seven species (32%) have become extinct in our North Wales study region in the last 150 years (Williams 1864; Ellis 1950). Based on reconstructed changes in land use (table 3), estimated declines in extant species have also been severe, ranging from 9 to 91% (table 2). There was no correlation between the existing British distribution size (percentage of 10 km squares populated) and percentage declines within our study region, either including or excluding the species that have become regionally extinct (arcsine-transformed data $r = 0.313$ and $r = -0.344$, respectively, d.f. $= 18$ and 11 and $p > 0.1$ in both cases). Thus, nationally widespread species have declined just as much within the North Wales region as more restricted species, even though previous analyses based on the national 10 km grid have indicated that localized species have suffered higher percentage declines (Heath *et al.* 1984; Thomas 1994; Thomas & Abery 1995). Coarse-grained maps grossly underestimate population-level rates of decline, particularly for common species that initially have many populations per grid square (Thomas & Abery 1995; Warren *et al.* 1997). Decline rates per unit area may be comparable for widespread and localized species, but localized species initially occupy much smaller total areas (table 1 and figure 1). Localized species are therefore particularly susceptible to regional (table 2) or species extinction (Gaston 1996).

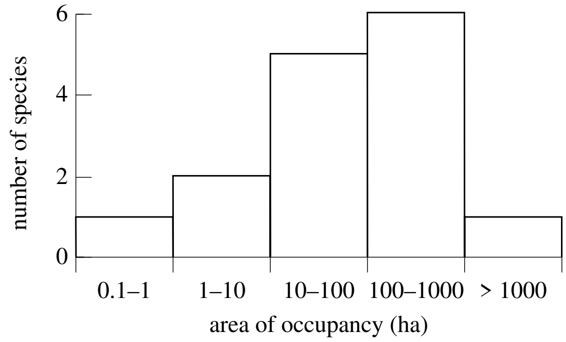

Figure 3. Frequency histogram of area of occupancy for all extant colonial butterfly species in a 35 km^2 area of North Wales (skewness relative to log-normal distribution $= -1.35$, $n = 15$ and $p < 0.05$).

(d) *The frequency distribution of flight areas*

The frequency distributions of flight areas are unimodal at a regional scale (figure 3) and approximately log normal: the same pattern has been demonstrated using coarse resolution distributions from other taxa in other regions (Gaston 1996, 1998). Because per unit area losses are not correlated with initial status (above), further habitat losses would tend to shift the entire frequency distribution towards smaller areas and eventually render species near the mode of the current distribution vulnerable to regional extinction.

If these patterns are replicated over larger areas (as seems probable) (Gaston 1996, 1998), shifts in entire frequency distributions towards smaller areas will probably lead to accelerating species-level (and higher level) (McKinney 1998) rates of extinction. In other words, for every critically endangered species that becomes extinct, we can expect that more than one endangered species will need to be reclassified as critically endangered. Of course, this will not be universally true, because there will be some increases in some landscapes over some time periods. Nonetheless, the implication is that population-level conservation is important for a wide range of species, not just for those that are already listed as critically endangered (Hughes *et al.* 1998).

We thank Nigel Bourn and volunteers at Butterfly Conservation, Liz Howe at the Countryside Council for Wales and Caroline

Bulman, Robert Wilson, Jorge Leon, David Gutierrez and Ilkka Hanski. The work was supported by NERC (Large-Scale Processes in Ecology and Hydrology) grant GST/04/1211. M. Cowley has a NERC Cooperative Award for Science and Environment studentship joint with Institute of Terrestrial Ecology.

REFERENCES

Cowley, M. J. R., Wilson, R. J., Leon-Cortes, J. L., Gutierrez, D., Bulman, C. R. & Thomas, C. D. 2000 Habitat-based statistical models for predicting the spatial distribution of butterflies and day-flying moths in a fragmented landscape. *J. Appl. Ecol.* (Submitted.)

Eales, H. T. 1996 *A revision of the status of the large heath butterfly* Coenonympha tullia *in Northumberland.* (Confidential report.) Wareham, UK: British Butterfly Conservation Society.

Ellis, G. 1950 Butterflies and moths of the local area. *Llandudno District Field Club Proc.* **22**, 21–25.

Fuller, R. M. 1987 The changing extent and conservation interest of lowland grasslands in England and Wales: a review of grassland surveys 1930–84. *Biol. Conserv.* **40**, 281–300.

Gaston, K. J. 1994 *Rarity.* London: Chapman & Hall.

Gaston, K. J. 1996 Species-range-size distributions: patterns, mechanisms and implications. *Trends Ecol. Evol.* **11**, 197–201.

Gaston, K. J. 1998 Species-range size distributions: products of speciation, extinction and transformation. *Phil. Trans. R. Soc. Lond.* B **353**, 219–230.

Groombridge, B. 1992 *Global biodiversity.* London: Chapman & Hall.

Heath, J., Pollard, E. & Thomas, J. A. 1984 *Atlas of butterflies in Britain & Ireland.* Harmondsworth: Viking.

Hughes, J. B., Daily, G. & Ehrlich, P. R. 1998 Population diversity: its extent and extinction. *Science* **278**, 689–692.

IUCN 1994 *IUCN red list categories.* Gland: IUCN Council.

Joint Nature Conservation Committee 1990 *Handbook for phase-1 habitat survey.* Peterborough, UK: Nature Conservancy Council.

Kunin, W. E. 1998 Extrapolating species abundance across spatial scales. *Science* **281**, 1513–1515.

Lawton, J. H. & May, R. M. 1995 *Extinction rates.* Oxford University Press.

Mace, G. M. & Lande, R. 1991 Assessing extinction threats: towards a revaluation of IUCN threatened species categories. *Conserv. Biol.* **5**, 148–157.

McKinney, M. L. 1998 Branching models predict loss of many bird and mammal orders within centuries. *Anim. Conserv.* **1**, 159–164.

Ordnance Survey 1901 *SH78/88 & SH77/87.* Southampton, UK: Ordnance Survey.

Ordnance Survey 1994 *Pathfinder 736 SH78/88 & SH77/87.* Southampton, UK: Ordnance Survey.

Pollard, E. & Yates, T. J. 1993 *Monitoring butterflies for ecology and conservation.* London: Chapman & Hall.

Prendergast, J. R., Quinn, R. M., Lawton, J. H., Eversham, B. C. & Gibbons, D. W. 1993 Rare species, the coincidence of diversity hotspots and conservation strategies. *Nature* **365**, 335–337.

Quinn, R. M., Gaston, K. J., Blackburn, T. M. & Eversham, B. C. 1997 Abundance-range size relationships of macrolepidoptera in Britain: the effects of taxonomy and life history variables. *Ecol. Entomol.* **22**, 453–461.

Ravenscroft, N. O. M. 1993 *A review of chequered skipper sites in Scotland 1993.* (Confidential report.) Wareham, UK: British Butterfly Conservation Society.

Samways, M. J. 1994 *Insect conservation biology.* London: Chapman & Hall.

Thomas, C. D. 1983 The ecology and status of *Plebejus argus* in NW Britain. Unpublished MSc thesis, University of Wales, Bangor.

Thomas, C. D. 1994 Local extinctions, colonizations and distributions: habitat tracking by British butterflies. In *Individuals, populations and patterns in ecology* (ed. S. R. Leather, A. D. Watt, N. J. Mills & K. F. A. Walters), pp. 319–320. Andover: Intercept Ltd.

Thomas, C. D. & Abery, J. C. G. 1995 Estimating rates of butterfly decline from distribution maps: the effect of scale. *Biol. Conserv.* **73**, 59–65.

Thomas, C. D. & Hanski, I. 1997 Butterfly metapopulations. In *Metapopulation biology: ecology, genetics and evolution* (ed. I. Hanski & M. E. Gilpin), pp. 359–386. London: Academic Press.

Thomas, J. A. 1983 A quick method of estimating butterfly numbers during surveys. *Biol. Conserv.* **27**, 195–211.

Thomas, J. A. 1992 The conservation of butterflies in temperate countries: past effort and lessons for the future. In *The biology of butterflies* (ed. R. I. Vane-Wright & P. R. Ackery), pp. 533–551. London: Academic Press.

Thomas, J. A., Thomas, C. D., Simcox, D. J. & Clarke, R. T. 1986 The ecology and declining status of the silver-spotted skipper butterfly (*Hesperia comma*) in Britain. *J. Appl. Ecol.* **23**, 365–380.

Vane-Wright, R. I., Humphries, C. J. & Williams, P. H. 1991 Systematics and the agony of choice: what to preserve? *Biol. Conserv.* **55**, 235–254.

Wain, M. 1997 *Large heath survey of Cumbria 1996.* (Confidential report.) Wareham, UK: British Butterfly Conservation Society.

Warren, M. S. 1992 Butterfly populations. In *The ecology of butterflies in Britain* (ed. R. H. L. Dennis), pp. 73–92. Oxford University Press.

Warren, M. S. 1994 The UK status and suspected metapopulation structure of a threatened European butterfly, the marsh fritillary *Euphydryas aurina*. *Biol. Conserv.* **67**, 239–249.

Warren, M. S., Baker, N. R., & Oates, M. R. 1995 *High brown fritillary: site dossier for Britain.* (Confidential report.) Wareham, UK: British Butterfly Conservation Society.

Warren, M. S., Barnett, L. K., Gibbons, D. W. & Avery, M. I. 1997 Assessing national conservation priorities: an improved red list of British butterflies. *Biol. Conserv.* **82**, 317–328.

Williams, T. 1864 *Complete guide to Llandudno.* Llandudno, UK: Thomas Williams.